

Sexual Dimorphism in the Pelvic Midplane and Its Relationship to Neandertal Reproductive Patterns

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ABSTRACT The fragmentary nature of the fossil record has limited the analysis of the Neandertal pelvis to the superior pubic ramus and the pelvic inlet. From an obstetric viewpoint, the pelvic midplane or “plane of least dimensions,” defined by the distance between the ischial spines, must be considered in the analysis of hominid reproduction. We examined the relationship between BSD and weight in a mixed sex hospital population undergoing diagnostic computed tomography (CT) scans (41 females and 40 males). Because femoral head diameter squared (FH^2) has been used as a proxy for weight in skeletal populations, it was also analyzed with respect to BSD and weight. Bivariate regression analysis of BSD with other body dimensions indicates the presence of significant sex differences. In females, but not in males, weight is a statistically significant predictor of BSD. FH^2 is an even better predictor of BSD in females while nonsignificant in males. Although weight and FH^2 are significantly correlated with BSD in females, FH^2 does not predict weight in females as well as it does in males. The positive correlation between skeletal frame size and BSD in females is indicative of an evolutionary pattern that must take into account the pressures of reproduction. Our results indicate that critical dimensions of the pelvis must increase as the maternal skeleton becomes larger. These results provide a context for the interpretation of the reproductive patterns of a relatively robust hominid population like the Neandertals. © 1996 Wiley-Liss, Inc.

The observation that the Neandertal superior pubic ramus is elongated and thin in cross-section (McCown and Keith, 1939; Stewart, 1960; Smith, 1976; Trinkaus, 1976) compared to that of modern humans has led to the construction of a number of theories concerning Neandertal reproductive patterns (Anderson, 1989; Brothwell, 1975; Dean et al., 1986; Greene and Sibley, 1986; Rosenberg, 1988; Trinkaus, 1984, 1990; Wolpoff, 1980). Wolpoff (1980) proposed that a longer superior pubic ramus contributed to a larger pelvic inlet which, in turn, corresponded to a relatively larger neonate cranium. Subsequent interpretations, based on the morphology of the Neandertal pelvis,

have included the prolonged gestation length model (Trinkaus, 1984) and the accelerated fetal growth model (Dean et al., 1986).

The most recent contribution to these functional interpretations of Neandertal pelvic morphology is Rosenberg's maternal weight model (1988). Building on the finding that maternal body weight is a critical determinant of birth weight (Garn and Pesick, 1982), Rosenberg examined the relationship between maternal body weight and pelvic

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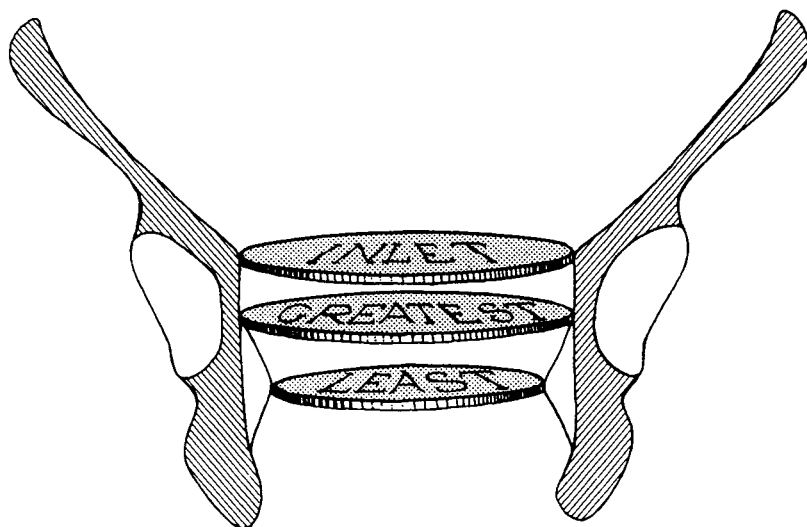


Fig. 1. Plane of least dimensions in the obstetric pelvis. (Reproduced from Oxorn-Foote, 1986, with permission of Appleton-Century-Crofts, Norwalk, CT.)

inlet dimensions. Her data suggested that populations with the highest relative weight, like the Zuni, possess the longest pubic bones. Although no modern human population has pubic bone dimensions that match those of Neandertals, it is unlikely that any modern human population is as heavy relative to their stature as the Neandertals. Therefore, Rosenberg suggested that Neandertal infants were the same size at birth relative to their mothers as modern infants. Her model linked superior pubic ramus length and birth weight to the absolute and relative weight of the mother. Consequently, Rosenberg concluded that the reproductive patterns of Neandertals and modern humans are similar.

The fragmentary nature of the fossil record has dictated that interpretations of the Neandertal pelvis and reproductive patterns rely solely on the pelvic inlet and its corresponding structures. However, the emphasis on the pelvic inlet in these reconstructions is of limited use from an obstetric perspective. Although the pelvic inlet becomes contracted in response to nutritional stress during development, it is the pelvic midplane (Fig. 1), the narrowest point in the birth canal, that interferes with the birth process in most populations (Sibley et al., 1992; Oxorn-Foote,

1986; Floberg et al., 1986, 1987). The distance between the ischial spines, or bispinous diameter (BSD), defines the obstetric "plane of least dimensions" (Oxorn-Foote, 1986). Projecting into the birth canal, the ischial spines provide support for the anal sphincter and for the abdominopelvic organs to resist intraabdominal pressure. The muscles and fascia of the pelvic floor insert directly or indirectly onto the ischial spines. Thus, according to Abitbol, "the ischial spines in humans pose the most serious threat to obstetrical delivery of any single feature of the human pelvis" (1988:58).

Unfortunately, ischial spines are not preserved in the Neandertal pelvic samples. The only reasonably complete Neandertal pelvis (Kebara 2) lacks ischial spines and is a male (Rak, 1990; Rak and Arensburg, 1987; Tague, 1992). Further, the appropriateness of attributing this specimen to the Neandertals recently has been the subject of debate (Arensburg, personal communication). In the absence of completely preserved Neandertal ischial spines, modern human data provide a context through which Neandertal pelvic relationships may be inferred.

To provide a reference for the interpretation of Neandertal pelvic morphology, we examine the pelvic midplane (BSD) in a mod-

TABLE 1. *Sample*

	Females	Males
n	41	40
Age range (average)	23–72 (47)	24–70 (49)
Weight range (average) in kilograms	41–104 (64)	57–118 (82)
Height ¹ range (average) in centimeters	152–175 (162)	165–188 (178)
Ethnicity	54% European	49% European
	10% African-American	7% African-American
	3% Asian	44% unknown
	33% unknown	

¹For height, n = 27 females and 23 males.

ern sample. BSD constrains the descent of the fetus through the pelvis during birth. Thus, birth of large neonates should require a correspondingly large maternal BSD. Although BSD has been analyzed extensively in the obstetric literature in terms of its contribution to fetal-pelvic disproportion (e.g., Jagani et al., 1981; Oxorn-Foote, 1986; Morgan et al., 1986; Thurnau and Morgan, 1992), the relationship of the pelvic midplane to maternal anthropometrics has not been systematically investigated. Because maternal weight is a strong predictor of birth weight (Garn and Pesick, 1982), we propose that selective forces acting on the female pelvis would favor a strong correlation between BSD and weight in females. To test a generalized maternal size–pelvic midplane hypothesis and to examine whether a particular component of maternal weight (i.e., bone mass, metabolic stores, height) may underlie this correlation, we analyzed the relationship between BSD and the following anthropometric measures: weight, height, body mass index (BMI), and skeletal frame size.

Femoral head diameter squared (FH^2) is used in this study as a proxy for skeletal frame size. Because it is the articular surface of a weight-bearing joint, many authors have used the femoral head as an index of body size in skeletal specimens (McHenry, 1976; Jungers, 1988; Rosenberg, 1988). Ruff and colleagues (1991) have shown that the femoral head remains constant relative to femoral cortices despite lifetime weight fluctuations. Thus, the femoral head can be of use in distinguishing soft vs. bony components of weight in the mixed age sample of known weights. Skeletal frame size is not a measure of bone density. We propose that larger values of FH^2 are indicative of overall bone mas-

siveness, while smaller values indicate relative gracility or slowness of the skeletal frame.

Because the pelvic inlet has been the focus in reconstructions of Neandertal reproductive patterns (Anderson, 1989; Brothwell, 1975; Dean et al., 1986; Greene and Sibley, 1986; Rosenberg, 1988; Trinkaus, 1984, 1990; Wolpoff, 1980), we also analyzed the relationship between the pelvic inlet and midplane. Males serve as a reference for non-specific effects of body size on pelvic geometry, as they are not directly subject to selective pressures imposed by parturition.

METHODS

We measured pelves from computed tomography (CT) scans from 41 females and 40 males undergoing diagnostic studies at the Hospital of the University of Pennsylvania (Table 1). Subjects ranged in age from 23–72 years with a mean of 48 years. CTs were taken on the subjects for a variety of reasons including trauma and for the diagnosis of specific disease states. All subjects included in the sample have fused bones lacking pathologies or age-related degenerative changes. The following exclusion criteria were used to determine an appropriate study sample: individuals indicating that they had experienced weight loss or gain of 20 pounds or more in the past 6 months, those who were extremely obese or lean as defined by the ninety-fifth and fifth centiles from the National Health and Nutrition Examination Survey (NHANES) standards (Frisancho, 1990), and patients identified as having end-stage illness.

Before measurements were taken, the following methods were explored to ascertain

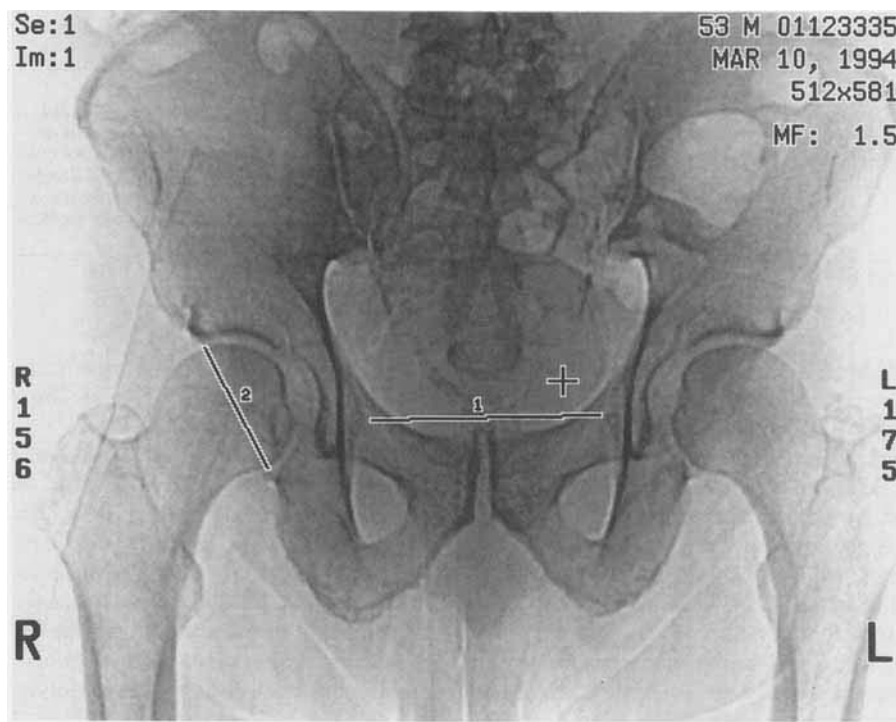


Fig. 2. Scout CT scan of pelvis illustrating (1) bispinous diameter, distance between the ischial spines (BSD), and (2) femoral head diameter, maximum diameter of the femoral head (FH).

the optimal technique for measurement of the pelvic midplane. Plane anteroposterior X-ray was found to be unsuitable for this study because of magnification error. The distance from the X-ray source to the ischial spines to the film is variable depending on the amount of soft tissue in the gluteal region of the subject. Because of this variable factor, the calculation of case-specific magnification could not be accomplished without exposing the subjects to additional lateral X-rays. Ultrasound technology also was found to be unsuitable because the ischial spines were not visible.

Computed tomography proved to be the most reliable method for measuring the pelvic midplane (Fig. 2). Because the subject is exposed to radiation from a 360 degree radius, it is possible to reconstruct mathematically an anatomically accurate image of the skeleton and other tissue structures (Thurnau and Morgan, 1992). "Scout" films resembling conventional anteroposterior X-ray images are used to determine the de-

sired distance interval between axial sections necessary to image specific structures in cross-section. However, with regard to the pelvic midplane, the position of the subject affects the probability of capturing both of the ischial spines in a single axial section. Even if the spines are present in a single section, it is difficult to determine which portion of the spine is observed (Aronsen and Kier, 1991). Because it is only the most distal portions of the spines that are measured when deriving the BSD, scout CTs instead of axial sections were used for measurement in this study.

The accuracy of the measurements taken from scout films was verified by the comparison of these same measurements taken from a modern bony pelvis with calipers (Fig. 3). Measurement error was less than 1% for each value. In addition to BSD, we measured acetabulo-symphyseal length (PAC) and transverse diameter (TD) of the pelvic inlet (Table 2). PAC was measured from the most superio-medial aspect of the pubic symphy-

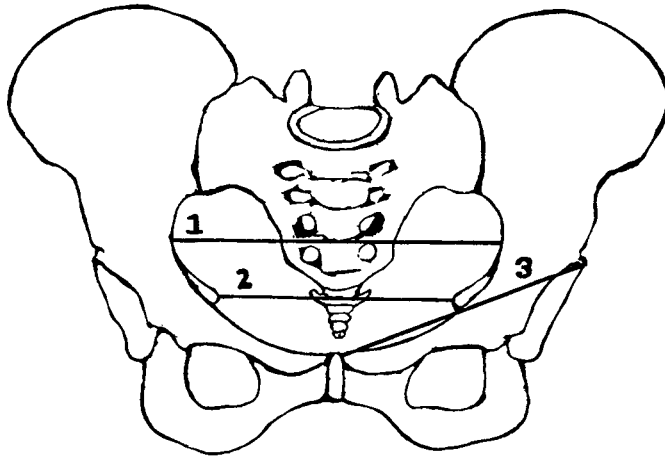


Fig. 3. Transverse diameter (1), the maximum distance of the pelvic inlet from a medio-lateral perspective (TD); bispinous diameter (2) (BSD); and acetabulo-symphyseal length (3), the most superior-medial aspect of the pubic symphysis to the most superior aspect of the acetabulum (PAC).

TABLE 2. Ranges and averages of pelvic and femoral head measurements in millimeters

	Females	Males
Bispinous diameter range (average)	83–112 (100)	68–94 (80)
Transverse diameter of pelvic inlet range (average)	111–147 (128)	95–137 (113)
Acetabulo-symphyseal length range (average)	92–126 (107)	93–120 (108)
Femoral head range (average)	36–48 (41)	42–55 (48)

sis to the most superior aspect of the acetabulum. This CT approach precluded measurement of the pubis from its termination in the acetabulum, used in classic studies of pelvic morphology (Washburn, 1948, 1949; Hanna and Washburn, 1953), but proved highly reproducible. In this regard, the PAC values derived in this study are not directly comparable to the published Neandertal pubic bone values because the acetabulum is missing in many of these specimens (Trinkaus, 1984; Rosenberg, 1988). TD is defined as the maximum distance of the pelvic inlet from a medio-lateral perspective.

To quantify skeletal frame size, we measured the maximum diameter of the femoral head using the technique of Ruff and colleagues (1991). Following Rosenberg (1988), this value was squared (FH^2) as an index of the area of this weight-bearing joint. Because weight was recorded for all 81 of our subjects, we also tested the utility of femoral head as a proxy for body weight. In addition, we tested the potential differences in the

ability of FH , FH^2 , and FH^3 to predict body weight in order to compare the power of this measure as a diameter, an area, and a volume. All skeletal measures were taken three times and then averaged.

In addition to these skeletal measures, we derived the body mass index (BMI) by dividing weight in kilograms by height in centimeters squared for those individuals whose height was recorded (27 females, 23 males).

RESULTS

Bivariate regressions of BSD with other body dimensions are reported in Table 3. Absolute weight is a significant predictor of BSD only in females ($P = .01$, $R^2 = .15$). Neither relative weight, as defined by BMI, nor height serve as significant predictors of BSD in either sex. However, in females P values for regressions of BSD with height and BMI approach significance.

Skeletal frame size, represented by FH^2 , is the most powerful independent predictor

TABLE 3. Bivariate regressions of bispinous diameter with other body dimensions

	Females		Males	
	R ²	P	R ²	P
Weight (kilograms)	.1503	.0123*	.0445	.1973
Height (centimeters)	.1393	.0552	.1350	.0925
Body mass index (weight/height ²)	.1315	.0630	.0077	.6982
(Femoral head diameter) ² (millimeters) ²	.5289	<.0001**	.0498	.1722
Transverse diameter (millimeters)	.4453	<.0001**	.1744	.0242*
Acetabulo-symphyseal length (millimeters)	.4962	<.0001**	.1622	.0111*

**P* < .05.
 ***P* < .01.

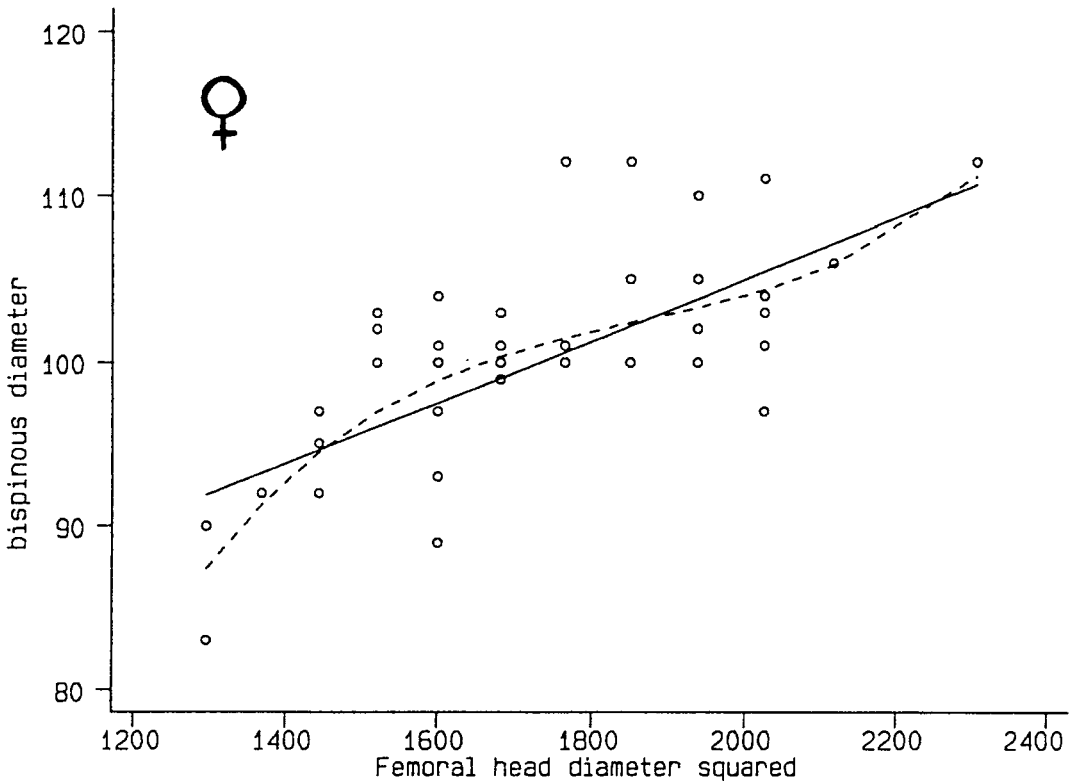


Fig. 4. Bivariate regression of femoral head diameter squared (FH²) and bispinous diameter (BSD). In females, a highly significant linear relationship exists between FH² and BSD (*P* < .001, *R*² = .53). FH² explains 10% more of the variation in BSD when a curvilinear regression with a third-order polynomial is used (*R*² = .58).

of BSD in females (*P* < .001, *R*² = .53). Conversely, no relationship exists between BSD and FH² in males (*P* = .17, *R*² = .05).

The relationship between FH² and BSD for females and males is graphically illustrated in Figures 4 and 5. These figures show a positive linear relationship between FH² and BSD only in female pelvis. Moreover, a third-order polynomial best describes this

relationship in that it comprises the reduction in variability in BSD values at extreme ends of the FH² range. The *R*² value for the curvilinear model is 10% more powerful than the linear model (*R*² = .58 vs. .53).

In contrast to the female pattern, male BSD values are randomly distributed across the entire FH² range. Accordingly, the regression line shown in Figure 5 does not sig-

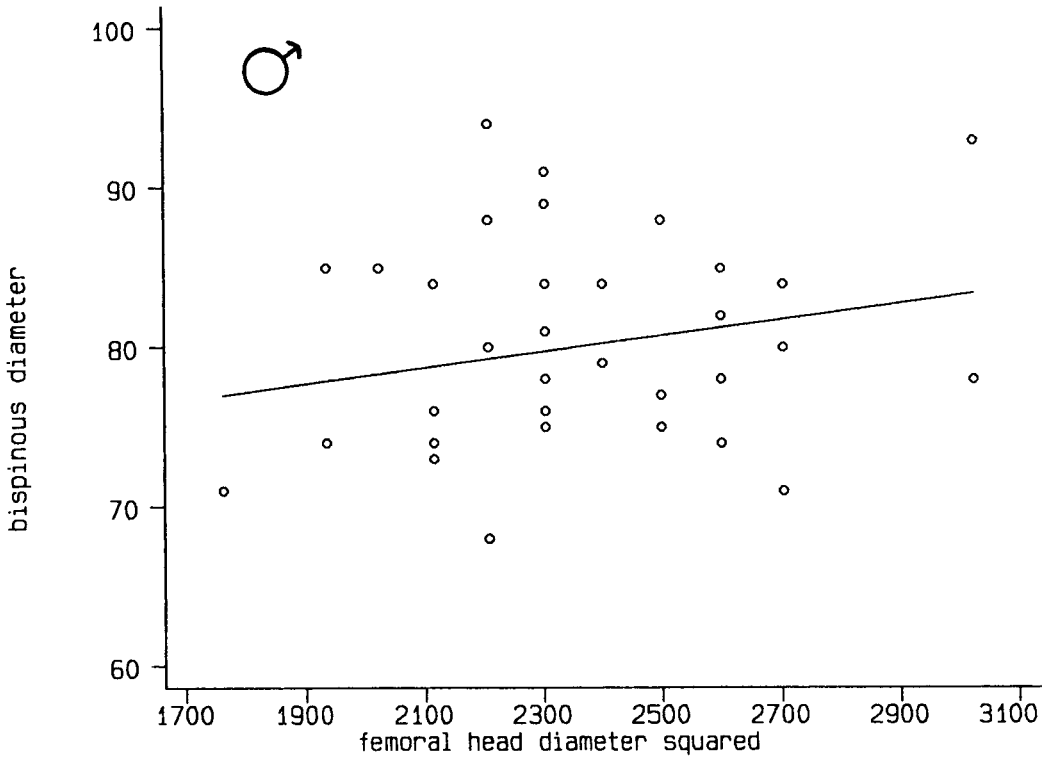


Fig. 5. Bivariate regression of femoral head diameter squared (FH^2) and bispinous diameter (BSD) in males indicating no association.

nificantly characterize the relationship between FH^2 and BSD in males.

The distributions of residuals from the bivariate regressions of BSD and FH^2 in males and females are presented in Figure 6. Female BSD variation is limited to the middle values of FH^2 . In contrast, male BSD varies throughout the entire range of FH^2 values. In other words, in contrast to females, the dimensions of male BSD may vary even at the extreme ends of the FH^2 range.

Acetabulo-symphyseal length (PAC) and transverse diameter (TD) of the pelvic inlet are significant predictors of BSD in both sexes (Table 3). Yet both of these skeletal measures account for nearly three times the amount of variance in BSD in females compared to that of males. Male BSD deviates from the pattern of increasing pelvic inlet dimensions produced by general scaling effects, while female BSD adheres closely to this pattern.

In Table 4, bivariate regressions of weight and FH^2 with pelvic inlet dimensions are reported. Weight and FH^2 correlate with PAC and TD at statistically significant levels in both sexes ($P < .01$). By contrast, the significant association between the size variables, weight, and FH^2 and the pelvic midplane is found only in females (Table 3).

The ability of femoral head diameter (FH) to predict body weight was tested. Although Rosenberg (1988) employed the area of a weight-bearing joint (FH^2) in her study, she suggested that FH^3 may more accurately index body weight because weight reflects a volumetric measure. Bivariate regressions of known body weight with FH, FH^2 , and FH^3 are presented (Table 5). Our results indicate that no significant difference exists in the ability of any of these femoral head values to predict body weight. In all three cases, the femoral head is nearly three times more powerful for predicting weight in males than

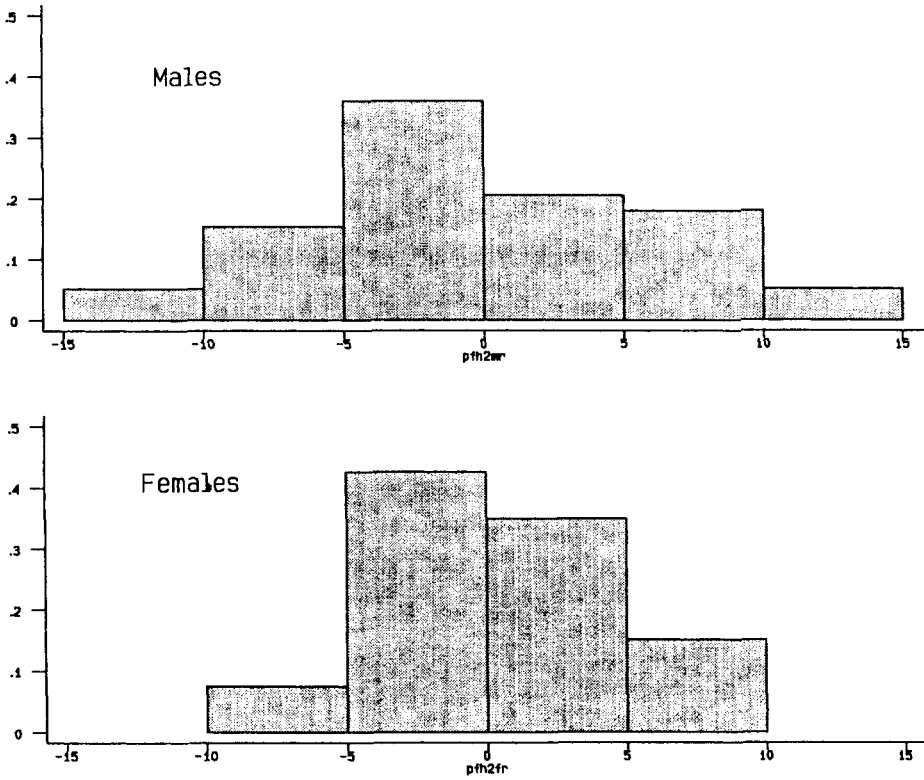


Fig. 6. The distribution of residuals from regressions of BSD predicted by FH^2 demonstrate sex-specific patterns. In females, residual distribution is entirely limited to the middle of the FH^2 range.

TABLE 4. Bivariate regressions of weight and (femoral head diameter)² with pelvic inlet dimensions

	Females		Males	
	R ²	P	R ²	P
Weight				
Transverse diameter	.2764	.0004	.2275	.0077
Acetabulo-symphyseal length	.1652	.0084	.2869	.0004
(Femoral head diameter) ²				
Transverse diameter	.3876	<.001	.3179	.0012
Acetabulo-symphyseal length	.4785	<.001	.4654	<.001

TABLE 5. Bivariate regressions of body weight with femoral head diameter, (femoral head diameter)², and (femoral head diameter)³

	Females		Males	
	R ²	P	R ²	P
Femoral head diameter	.1420	.0165	.4084	<.0001
(Femoral head diameter) ²	.1429	.0162	.3977	<.0001
(Femoral head diameter) ³	.1437	.0159	.3858	<.0001

females. Male values are highly significant at the $P < .01$ level, while female results are significant at only the $<.05$ level.

DISCUSSION

Because of the limitations of the fossil record, reconstructions of Neandertal reproductive patterns rely on the dimensions of the superior pubic ramus and inferred pelvic inlet size. We redirect the emphasis of these reconstructions to the midplane or plane of least dimensions. This study identifies the pelvic midplane, reflected in BSD, as a locus of sexual dimorphism resulting from the selective pressure of parturition on female pelvic anatomy.

Pelvic inlet vs. pelvic midplane

In the present study, we address the impact of weight and skeletal frame size on the dimensions of the pelvic midplane and inlet. BSD is the only pelvic measurement affected

by weight and skeletal frame size (FH^2) in a gender-specific manner. In contrast, the pelvic inlet of both males and females, represented by PAC and TD, responds similarly to increases in weight and FH^2 . It appears that the relationship between these inlet dimensions and either weight or FH^2 reflects scaling effects that impact both sexes equally. In contrast, gender-specific relationships between BSD with both weight and FH^2 provide evidence for selective pressures of parturition acting on female pelvic geometry. These results support previous studies which highlight the importance of the pelvic midplane, rather than the inlet, in reconstructions of reproductive patterns (Greene and Sibley, 1986; Abitbol, 1988; Tague, 1992).

In the reconstruction of Neandertal reproductive patterns, the complexity of the relationship between pelvic geometry and both reproduction and bipedalism must be considered. The length of the superior pubic ramus and its contribution to the dimensions of the pelvic inlet in Neandertals may have been associated more strongly with the pressures of locomotion, posture, (Rak and Arensburg, 1987) or overall body size (Greene and Sibley, 1986; Frayer, 1988) rather than with the requirements of reproduction (Wolpoff, 1980; Trinkaus, 1984; Dean et al., 1986; Rosenberg, 1988).

The presence of an elongated superior pubic ramus in both Neandertal sexes and even in the juvenile specimen La Ferrassie 6 led many researchers to consider these traits to be genetically determined (Frayer, 1988) and unique to the Neandertals, given their proposed reproductive adaptation (Tompkins and Trinkaus, 1987). However, the earlier hominid specimens with preserved pubic bones, namely an *A. afarensis*, Al-288-1, and an *A. africanus*, Sts-14, also show elongated superior pubic rami as well as a somewhat platypelloid pelvic inlet (Lovejoy et al., 1973; Tague and Lovejoy, 1986). The interpretation of the pelvic morphology of Sts-14 is less straightforward than that of Al-288-1 because its left pubic bone is distorted (Day, 1973). Although the sample size consists of two specimens from distinct species, Frayer (1988) suggested that the australopithecines may have had long pubes in spite of the fact

that they did not give birth to big-brained babies. The only other specimen with partially complete pelvic morphology, WT-15000, a *H. erectus*, has been described as having a large transverse diameter of the pelvic inlet (Walker and Ruff, 1993). Though the inlet has been reconstructed without the benefit of preserved pubes, the inferred presence of elongated superior pubic rami in this juvenile male specimen may be interpreted as a plesiomorphy and have little to do with increasing neonate cranial dimensions through time (Abitbol, 1991; Frayer, 1988). Although the pelvic inlet and midplane are both dimensions of the birth canal, a reinterpretation of the fossil record with respect to the results of the present study suggests that the pelvic midplane rather than the inlet is the critical dimension for successful birth.

Absolute weight vs. skeletal frame size

Our results indicate that skeletal frame size, rather than weight, has a greater impact on the dimensions of the female pelvic midplane. Skeletal frame size as indexed by FH^2 is a more powerful predictor of BSD in females than height or weight. The emphasis on skeletal frame size rather than weight represents a refinement of Rosenberg's maternal weight model (1988). By focusing on one of the constituents of body weight, this study is able to address more directly the relationship between skeletal size and bony constraints of the pelvis. Given our results, maternal skeletal frame size appears to be a critical factor in determining the female pelvic dimensions that constrain the birth process.

The distribution of BSD values for specific measures of FH^2 show a female-specific pattern that is suggestive of stabilizing selection. Until more data are gathered, it appears that the female pattern is defined by random variation in BSD around the middle portion of the FH^2 range, whereas variability is reduced at the extreme ends of this range. Although the data presented in this study do not address the relationship between skeletal frame size and neonate size, they indicate that skeletally large women must have a correspondingly enlarged pelvic midplane. It may be inferred that an enlarged BSD is related to overall larger neonate sizes

for skeletally large and relatively heavier females.

The male pelvis is not directly exposed to the selective pressure of parturition. Consequently, male BSD variability is not constrained by specific values of FH^2 . Male skeletal frame size and the dimensions of the pelvic midplane are unrelated. Male ischial spines may increase in size and change in orientation without any compensatory adjustments in order to prevent a bony impingement into the birth canal.

Application to the fossil record

The finding that FH^2 is a powerful predictor of female BSD is particularly useful in the context of the fossil record where body weight is unknown for even the most complete skeletal remains. In skeletal populations, weight traditionally has been estimated by some bony parameter such as the femoral head diameter (McHenry, 1976; Jungers, 1988; Rosenberg, 1988). As weights were known for all subjects in this study, we tested the reliability of predicting body weight from femoral head diameter. Bivariate regressions of weight with femoral head diameter indicate that this estimate is more reliable in males than in females (Table 4). This discrepancy between the sexes may be accounted for by the differences in the constituents of weight for males and females (Ruff et al., 1991). These data show that skeletal frame size rather than body weight dictates pelvic midplane dimensions in females. The ability to rely solely on bony measures in the reconstruction of reproductive processes minimizes the potential error inherent in body weight inferences from skeletal material.

Because FH^2 values of Neandertal females with associated pelvic remains (Rosenberg, 1988) fit within the range of our female sample, these data are particularly relevant to the reproductive patterns of the Neandertals. The success with which Neandertal FH^2 predicts BSD is even more likely given the reduced levels of variability at the extreme ends of the range in the present study and the observation that articular surface size has remained relatively constant through evolutionary time (Ruff et al., 1993). Using the regression equations generated with the

femoral head data presented here, BSD for these Neandertal specimens would fall within the upper portion of the modern human range. Female Neandertal femoral heads with associated pelvic remains such as Krapina 208 ($FH = 47$ mm) and Tabun C1 ($FH = 43$ mm) (Trinkaus, 1984) predict BSD values of 108 and 102, respectively.

In this study, we established the similarity between male and female pelvic inlet morphology in its response to absolute and relative weight and skeletal frame size. We have also determined that superior pubic ramus length and transverse diameter explain nearly three times as much of the variability in female BSD compared with that of males. Given these observations from a modern human sample, we suggest that the elongated superior pubic ramus in the Neandertals may be interpreted as a compensatory adjustment to provide adequate BSD in females from a skeletally large and heavy population.

CONCLUSIONS

We suggest that knowledge of pelvic adaptation to parturition in modern humans may facilitate the interpretation of the reproductive patterns and pelvic morphology of Neandertals. Two observations pertinent to pelvic structural adaptation to birth are 1) the positive correlation between maternal and fetal size and 2) the obstetric significance of the pelvic midplane or BSD as the narrowest point in the birth canal. The female-specific correlation between BSD and body size is consistent with the reproductive function of the female pelvis. In contrast, male BSD varies widely with changes in overall body size. Although weight has a significant impact on the female pelvic midplane, BSD is more highly correlated with maternal skeletal size as indexed by FH^2 . In addition, FH^2 is a better predictor of weight in males than in females, indicating that the use of FH^2 to estimate female body weight from skeletal samples may be unreliable. However, it appears that relative skeletal frame size has a greater impact on bony interrelationships and dimensions in the pelvis than does maternal weight, thereby reducing the importance of constructing reliable weight estima-

tions. The following are two issues raised by this study: 1) is relative skeletal frame size a better predictor of neonate size than weight?, and 2) might a similar relationship between FH^2 and BSD hold for Neandertal or other skeletal remains? Until more complete fossil evidence becomes available, estimates of Neandertal female BSD may be derived from FH^2 values. Application of the skeletal frame size model may provide new insights into the Neandertal reproductive process.

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